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## **Feelings as agents of selection: putting Charles Darwin back into (extended neo-) Darwinism**

Running Title: Feelings as agents of selection

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This cross-disciplinary essay employs some illustrations ('vignettes') of behavioural interactions examined by the authors (man, mammals, fish, octopus) to show feelings and emotions (affects) acting as essential regulators of the process of living. The notion of the primacy of feelings as both necessary feed-backs operating in self-preservation and growth, and as agents of selection during inter-subjective and predator-prey exchanges, is supported by a wealth of human and comparative neuroscience findings. The trans-species core self of vertebrates, identifiable with ancient brain structures on or near the midline, and studies of the vasopressin/oxytocin (VP/OT) system that have uncovered a functional and epigenetic continuum traceable to pre-Cambrian times, helps to re-align evolutionary theory upon Darwin's original unabashed notion of a place for emotions, separate from 'cognitive' ideas.

**ADDITIONAL KEYWORDS:** physiology – evolution – emotion – process of living (POL) – learning and imprinting – cooperation – affective neuroscience – evaluation – head *versus* heart – meteoropathy.

## INTRODUCTION

The question of what role feelings and emotions have and have had in evolution of the biosphere is easily asked. And in one sense is easily answered. Feelings and emotions, as forms of *evaluation*, belong with the myriad other self-evaluating processes operating amongst living things and between living things and the environment. Thus they also belong with definitions of evolution as a self-regulatory (self-evaluating) process (see other contributions to the present volume).

A more difficult question is how to present such, on principle, philosophical argument in a way that has meaning for working biologists studying and measuring particular adaptations at the whole organism or cellular level. Whatever personal thoughts may be held about the place of feelings and emotions in the lives of animals, few biologists will belong to disciplines that address them directly. Psychology and physiology of the emotions belong with human studies; their history in ethology is very patchy<sup>1</sup>, and largely confined to questions of motivation, drive, stress and suffering. Today, as yesterday, when it comes to publishing results, biologists take care to avoid all reference to emotions, and to feelings, if only to steer clear of the many well known epistemological shoals they are not trained to navigate, and to remain within the framework of a discipline that has traditionally excluded them (Fig. 1).

Within theories of evolution, the entrenched place of ‘altruism’ as ‘cause’ in kin selection arguments does nothing to discourage the agnosticism. Yet it has long been known that intimate behaviours – as between infant and caregiver – are governed, not by degrees of genetic relatedness, but by physiological *mechanisms of attachment*<sup>2</sup>. That is by feelings. We shall see that the question is intertwined with that of *cooperation* (*cooperativity*, Packard, 2006). In his book detailing reciprocal relations between systems at many levels, Warder Clyde Allee (1931 [1978]) dedicated a final chapter to the principle of cooperation<sup>3</sup>. But for whatever reasons, not least cultural expectations and habits of thought (see Packard, 2013) this *primary principle in biology* has been subverted into something to be “explained” in terms of secondary principles. In gene-centred selection theory, the down-grading of the principle can take the form of denial: no trivial matter given the size of the theoretical literature portraying cooperation between individuals as a “problem” both for biological and social scientists<sup>4</sup>. Proponents of that internal logic seem to be unacquainted with the quorum sensing of bacterial colonies or equivalent cooperative phenomena at other levels of organisation (see Packard, 2006), and to be able to turn their backs on any affective content (intrinsic rewards) that the process of ‘working together’ might afford.

As we shall see in the Discussion, explicit reference to feelings is frequently also missing from social and cognitive interpretations of emergent evolution (Byrne & Bates, 2007). More generally, one looks in vain in the extended modern synthesis (EES: Carrol, 2000; Pigliucci, 2007) for any hint that biologists might learn about how things work in nature by reflecting on the fact that their own feelings and affects, which are at every point evaluating and selecting their own actions, have a physiological basis shared with other mammals and a common, 200-million-year phylogenetic history.

Fortunately, affective neuroscientists have come to the rescue (Panksepp, 2005; Panksepp & Northoff, 2009; Northoff & Panksepp, 2008). Emphasizing the

deep comparative roots and integrating role of emotions, drives, moods, appetites, etc, they distinguish carefully between the ‘affective’ components of behaviour (associated with ancient brainstem and corebrain centres, see below) on one hand and the ‘cognitive’ (outer cortical) components on the other. Jaak Panksepp (2000: 250) points out that the fashion of evoking the latter as a guiding force in evolution, while neglecting the former “emotional engine” (Starr, 2006), is a return to dualistic thinking<sup>5</sup>.

Maybe there is now a chance to turn the situation on its head. On graduating from university, the biology student has at best only a partial understanding of the doctrine of natural selection and limited direct experience of the adaptations that it attempts to account for. But all students have been through infancy and childhood. Well before morphogenesis established a cortical-brain network able to make intellectual sense of the world, mid-line core-brain structures laid down early in ontogeny and “shared across species” were meeting the vital needs of “the core self, which relates an organism’s interoceptive stimuli to its goal orientations (and the animate world’s exteroceptive stimuli)” (Northoff & Panksepp, 2008: 259).

The first two vignettes seek to tap the implicit understanding available in the “trans-species” roots of one’s own growth and development from babyhood: a scientific method, certainly used by Darwin, which belongs with the *gentle empiricism* (Zarte Empirie) of Goethe (Wahl, 2005) characterised by the observer empathising with the subject/object.

Setting aside the centuries-old Cartesian mind-body controversy and without attempting to review the huge literature, our central position is close to that of the philosophers Alfred North Whitehead (1925, 1929) and Susanne Langer (1967). Emphasis is on the organism rather than the species, and on organisation and togetherness rather than competition in the logic of life (cf. Williams & Fraústo de Silva, 2002, and Bruce, 2014; see Vincent, 1993, for an example of that logic in a discipline of direct interest to this essay).

Criticism of neo-Darwinian genetic determinism – still widely taught despite repeated exposure of its major fallacies (see Noble, 2011, 2013, for masterly summary) – takes the form of occasional reference to Haukioja’s neglected theory of living entities (“process of living” – POL) (Haukioja, 1982; see Appendix 1). The main aim of this essay is to anchor the process or physiological view of these entities<sup>6</sup> by way of a few challenging examples which can only be properly understood when feelings are granted a guiding role. A major weakness is that these ‘vignettes’ refer only to a small section of the animal kingdom where feelings have become reinforcers of individual learning and a medium of communication. Instead, we like to think that self-evaluation through the ‘felt element’ engaged with the environment from the beginning is a general and invariant process, and that it meshes with other integrating principles old and new operating at the organism/environment interface (see Appendix 1).

The three main parts of the paper – assorted vignettes showing the work of affect, an account of behaviour space and runaway evolution, and the extended discussion – reflect the personal history of an idea.

## THE WORK OF AFFECT: PUTTING DARWIN BACK INTO (EXTENDED NEO-) DARWINISM

Gary Larson's cartoon "*natural selection at work*" (Fig. 2)<sup>7</sup> illustrates two well established ideas: that in predator-prey relationships, predators, through their choices, are acting as selecting agents, and that with wolves, capture of prey is a matter of *cooperation* between individuals.

We examine what emotions might be involved in that social interaction and in the predator-prey relationship. We build the account upon three conceptual struts: *cooperation* and cooperativity as primary principle amongst cells and organisms, logically independent of altruism or other secondary principles; *feelings* as *logically prior to cognition*; and *selection* as in the ordinary choices made by organisms through affective evaluation, *i.e.* its "felt element" (Langer, 1967; Innis, 2009).

The appeal is for biologists to adopt Darwin's uncomplicated and liberating acceptance of emotions in animal existence (Darwin, 1872) "with his robust but scientifically disciplined common sense" (Huxley, 1966a: 250) – sometimes he calls them 'passions'<sup>8</sup> – and to see them, on a systems view, both as the integrators of behaviour and as so-called reference values in pattern-generating and pattern-recognizing feedbacks of behavioural ecology, thereby accounting for critical directions taken by evolution<sup>9</sup>.

### VIGNETTES

As preface to our first vignette introducing that double role:

A young cat of six months is ignoring her first litter born a couple of hours earlier. The instant a warm wet cloth was applied to her belly<sup>10</sup>, the whole behaviour of the animal – mood, posture, bearing towards the newly arrived objects – switched to the maternal.

What is observed here is a *global transformation* of the cat's emotional, affective state which at the same time is acting as the leading arm of a *feedback loop* promoting inter-subjective engagement between individuals. Obviously the sensory input is important, but the transformation cannot be meaningfully interpreted in simple stimulus-response terms (any more than it would be suitable to employ such terms to try to understand one's wife or daughter similarly affected) if only because of the several temporal scales involved (see Discussion).

Here is what Jaak Panksepp has to say about comparative aspects and the two-way relationship with human studies:

Considering the deep neuroanatomical homologies in the organization of subcortical regions of the brain, it is likely that our capacity to decipher the circuitry that generates emotional processes in animals (e.g., as indexed by approach and avoidance, and conditioned place preferences and aversions) can provide an essential platform for understanding which types of brain systems govern affective states, and perhaps the foundations of consciousness, in humans (Panksepp, 2000: 245)

[T]oo much of cognitivism is stuck with the belief-based view that external information-processing is the foundation of what organisms do, rather than the embodied emotional and motivational state that depend on large non-linear attractor landscapes, arising from below, that control bodily actions and associated feelings. In fact, there is probably an organismic centre, a core self process, for most things animals do. Information-processing revolves around an affectively self centred, 'What's in it for me?' type of process. If we gave those ancient systems primacy, I think we would have a dramatically different view of learning (J Panksepp, quoted in Gallagher, 2008: 103)

### *Milk-ejection reflex and mother infant bonding*

The experiment of blocking the sense of smell in a mother goat or other ungulate at parturition (Klopfer & Gamble, 1966; Klopfer, 1971) removes a vital step in the chain of events that establishes both suckling and emotionally guided exchanges with the newborn.

The neuro-endocrine pathways of the oxytocic (milk-ejection) reflex causing release of *oxytocin* and *vasopressin* into the blood stream and ejection of milk from the mammary glands have been known for a long time. Nerve impulses induced by stimulation of the mother's nipples are carried by synapses in the spinal cord and brainstem to the hypothalamus: the arc being completed by the firing of oxytocin cells in the hypothalamus (supraoptic nucleus) whose axon terminals secrete their products into the posterior pituitary (neurohypophysis).

What was not discovered until later decades is that the same hypothalamic neurones in the supraoptic nucleus are mediating the global emotional and behavioural changes associated with suckling – apparently even before the classic milk let down event (and other responses to the circulating hormones) just described – through an intricate network of dendrites ramifying from their cell bodies in the other direction: secreting the same neuropeptides into brain centres such as the amygdala (Sabatier *et al.*, 2003; Ludwig & Leng, 2006). Further integration of the responses necessary for recognition of the young is achieved by yet other populations of oxytocin- and vasopressin- secreting neurones intrinsic to the olfactory lobes of the brain: phylogenetically the oldest forebrain structures (Tobin *et al.*, 2010).

We include a Pompeian artist's mythical depiction (Fig. 3) of the resulting attitudes (motor behaviours) as it captures the reciprocity and essential feedback nature of the relationship, whilst choice of subjects – child and deer – betrays an ancient cultural awareness of taxonomic realities: that emotional bonding is ubiquitous, homologous and interchangeable amongst mammals.

### *Kamala the wolf-child (Fig. 4)*

Our second vignette of a spontaneous, if surprising, cross fostering experiment involving two human infants reared by a wolf mother<sup>11</sup> is a particularly spectacular illustration of the vital role that emotional bonding plays in promoting processes of development and growth. It constitutes the chief exemplar of numerous comparable, less well documented cross-fostering 'natural experiments' recorded in the literature (for extensive summary see Zingg RM, in Singh & Zingg, 1942: 131–379). Long

considered of great importance for anthropology, we hold them to be every bit as important for biology.

The main facts recounted in the first half of the book that includes Singh's transcribed 'Diary of the Wolf-children of Midnapore (India)' (Singh & Zingg, 1942: 1–126) are not disputed. Details rely on the trustworthiness of the diarist, vouched for by several authorities and by the internal evidence. Having reluctantly agreed to arrange their capture and take them to his orphanage, J.A.L. Singh found the children clutched together with other cubs in a tight 'monkey-ball' at the bottom of the wolf den. He reported them to be strong and healthy at the time of capture (in 1920), with estimated ages of 18 months and 8 years. The den had been fiercely defended by the presumed mother, shot dead with an arrow before digging could begin. The human children ran on all fours, ate raw meat and offal, possessed unusually developed jaws, eyes that shone in the dark (evidently they had developed a functional tapetum lucidum<sup>12</sup>) and asserted aggression by biting. For many months thereafter, they shunned human company seeking that of animals, lived at night and pined for their lost companions. "The cry was a peculiar one. It began with a hoarse voice and ended in a thrilling shrill wailing, very loud and continuous ..... Almost every night they used to cry regularly three times, once at about 10 o'clock and once at three o'clock in the morning" (Singh & Zingg, 1942: 45). About a year after capture, both children became seriously ill; the younger died.

The proximal requirement for the success of such an 'experiment', it is generally agreed, is that the mother wolf be lactating at the time she adopts an abandoned infant. But the case of Kamala and Amala (the names given them by Singh and his wife) also reminds us, first and foremost, that attachment (bonding) is a process well known to cross boundaries of species and order: even of *class* in the case of Lorenz's jackdaws and geese (Lorenz, 1935, 1952); second, that an ingredient – or 'glue' – is present, common both to the wolf mother and to the infants, so strong on the side of the infant that the development of all physiological systems (circadian, digestive, locomotory, vocal, olfactory, visual) was subordinate to the conditions of upbringing resulting from the attachment. In some ways it is the obverse of the deprivation experiment, with its well known failure to thrive in the absence of maternal affection (Spitz, 1945; Bowlby, 1969, 1973)<sup>13</sup>.

On the side of the wolf, "There, of course, is no reason", writes Pakenham-Walsh (Singh & Zingg, 1942: xxvi) in his Preface to the book "to think that Amala and Kamala were sisters, but it is distinctly interesting that a wolf-mother should have been so pleased with her experiment in rearing a human cub that she should later on adopt another".

### *Role of the affective component in imprinting and in habitat selection*

To proceed from this positioning of the affective component at the heart of the urge to live – without which human life loses its value – to the first reactions of a larval teleost towards potential prey may not be such a big step for the comparative anatomist and ethologist. The role of the felt element, or affective component, in

switching the individual from endogenous to exogenous feeding – as ‘appetite’, ‘hunger’ – is as crucial in the life of a fish as in the life of a baby<sup>14</sup>.

The key is in the details. The “visual grasp reflex” of a young herring (Fig. 5) evoked by encounter with a potential food item (Rosenthal, 1969) is – like the rooting reflex of the newborn infant – an innate releasing mechanism (IRM) relatively hard-wired in midbrain structures at hatching; but it is only activated in the days following emergence from the egg when the larval body has used up the yolk supply<sup>15</sup>, the nutritional state of the fish being presumably sensed by hunger and satiety cells in the ventro-medial hypothalamus. Like the search of an infant for the breast of the mother, the IRM is elaborated through the sensorimotor feedbacks of early experience once feeding starts; before yolk resorption, herring larvae are indifferent to such stimuli as food items present in the water (Kjørboe, Munk & Gatt Støttrup, 1985).

The timing of the first event, and subsequent imprinting on one food species rather than another (Rosenthal, 1969; Rosenthal & Hempel, 1969), also has wider, ecological repercussions upon the distribution and numbers of prey at any one time and location.

‘Appetite’ and ‘hunger’ are interoceptive universals limited in space and time. The affective component, cued by an external signal, also enables living entities to assess their fitness to survive over the much longer term. The ‘address’ of the home stream of a salmon, returning to breed where it was born, is imprinted in the fish at the smolt stage (Hasler & Scholz, 1983) and can be recorded electrophysiologically years later when adult, either at the single neuron level – or at the level of the enormously increased electroencephalogram activity and swimming activity it triggers when the individual returning from the sea encounters water with the same chemical composition as the home stream. The interest of this example is that the mechanism enables a salmon to recognize a particular habitat or refuge of proven value for its offspring through direct reference to the encoded experience of the parent when a juvenile: fitness being inferred from survival of the fish to date. Though the accompanying feelings cannot be recorded, at least the drive component can.

### *Octopus learning*

Our next vignette illustrates the role of the affective component in learning; it constitutes the ‘unconditioned stimulus’, positive or negative, at the heart of the Pavlovian method for establishing learning in the laboratory<sup>16</sup>. As used by JZ Young and his school (Young, 1961) to train *Octopus vulgaris* on visual or other discrimination tasks – for instance to distinguish between a black and a white target (compare Fig. 7) – it took the form of food ‘reward’, i.e. pleasant ‘taste’ via chemoreceptors to reinforce the natural readiness of an octopus to make sorties from its ‘home’ to investigate novel objects (‘conditioned stimulus’<sup>of the experiment</sup>), while ‘pain’ (electric shock perceived by nociceptors) served to inhibit such approaches<sup>17</sup>, mimicking the natural ‘experiment’ of this predatory animal engaged in exploring the outside world.



Figure 6, based on a filmed encounter between a small octopus and a crab in which the crab got the better of the exchange, illustrates the ‘natural’ role that *pain* (nociception) plays in the learning process on an evolutionary time line.

Well before coming into play as the crab’s exteroceptive ‘punishment’ of the predator – or as the experimenter’s positive or negative reward for action – the affective component is present in the interoceptive form of appetite for action. As with the larval fish example, hunger conditions the octopus’s decision to investigate/attack<sup>18</sup>.

Although no equivalent of the hypothalamus is known for location of the brain mechanisms of ‘drive’ and ‘appetite’ in *Octopus*, the barrier of ignorance does not hinder public perception of their capacities to feel. Octopuses have for the last 25 years been on the register of UK Home Office regulations governing experiments with living animals and, in a wider move by politicians and administrators, cephalopod workers in Europe are expected to be subject to similar legislation to that governing handling and experimentation with fish. Organisers of the Erice symposium on the subject of *fear* and defence in animals chose the octopus as the statutory invertebrate (Packard, 1990).

### *Conflicting emotions*

One of the spin-offs from the extensive programme of experiments with *Octopus vulgaris*, mentioned above, was the many specific behaviours (including attention, investigation, attack, withdrawal, conflict and displacement activity) observed over the years in individuals undergoing training through reward and punishment. They made a substantial contribution to our catalogue when we came to describe and classify the natural motor patterns exhibited by the species (Packard & Sanders, 1969, 1971), including dramatic expressions of colour and contrast at the level of the skin.

Figure 7 shows octopus as a picture of conflicting emotions, between desire to investigate (curiosity) and fear of being hurt, much like the conflict posture of a herring gull caught at the edge of its territory between attacking a neighbour and fleeing. Such ordinary language description receives scientific authority from knowing the immediate history of the individual in captivity, which can be manipulated by the experimenter, and the conflict enhanced: for instance by reversing the sign of the conditioned stimulus (*e.g.* delivering a shock, instead of reward) during the conditioning process or once a task has been learnt (‘reversal training’). Note that the whole body of the octopus is affected<sup>19</sup>.

Conflict may result in displacement activities and ritualisation (Packard, 1963: 44–46), processes that Tinbergen and others argued to be hugely important in the evolution of social relations and communication of intentions amongst animals (Tinbergen, 1951: 113–119, 1965, 1972; Huxley, 1966a; Baerends, 1975)<sup>20</sup>. Further ethological observations on these classical lines are long overdue. (For a summary of behavioural conflict and catastrophic physiological effects of thwarted drives quoting a fatal example, Barnett, 1964, see Manning & Stamp Dawkins, 1998: 246–254.)

*Meteo[ro]pathy: fundamental organism/environment reciprocity in behaviour space mediated by mood?*

Finally, an illustration that begs many questions. It lacks satisfactory physiological or medical explanation; on the other hand it has an adaptive (evolutionary) one. The phenomenon takes us, in theory, back to our palaeolithic selves and to the original relationship between physical and living worlds.

The word *mete[or]opathy* (sensitivity to weather) describes the subtle, sometimes dramatic, changes in mood, feelings of ‘wellness’, etc., experienced at the approach of a change in the weather: either for the ‘better’ or for the ‘worse’ (Packard, 2001)<sup>21</sup>. Like the weather states they mirror, manifestations vary over a wide range both qualitatively and geographically and are idiosyncratic. Many, perhaps most, people report no such experience, though they are known to provoke, at times, serious medical ailment (Lopez del Val *et al.*, 1991). Nevertheless the general phenomenon is probably universal; it clearly concerns core brain affective functions with global effect on an individual’s behaviour.

The best studied, and seriously debilitating, is the Föhn effect – “Chinook” in North America (Nkemdirim, 2007) – experienced by people living on the lee side of certain mountain ranges where catabatic [pseudo-adiabatic, Föhn] winds accumulate positive (static) electrical charge in excess of negative charge. From the perspective of affective neuroscience, the depression, lethargy, irritability, *etc.* experienced by so-called ‘pos-ion’ sufferers – or other packages of feelings (mood states) induced by changes in the weather – may be seen as equivalent to the meteorologically-conditioned affective states of other animals: for instance night restlessness in migratory species of birds, which can be measured as variations in behavioural activity (see below).

The global effect they have upon levels of motivation and subjects’ readiness to act – dictating stay-at-home or other adaptive behaviour in weather conditions threatening survival in a hunter-gatherer community – would then be seen to have been no less valuable ancestrally than it is in other animals. Such signs have certainly not been ignored by the evolutionary process any more than, on the longer term, and in a seasonal context, have rates of increase in day length predictive of spring and its affordances, or declining day-length heralding the rigours of winter, which are built into the physiology of a great many organisms. Though there seems to have been little work on the afferent, or perceptual, side of the global response – and surprisingly little scientific study generally considering its importance in every day life – there is every likelihood that signals from many different sensory sources, including static-electrical charge and ambient light levels, feed directly to, and are being integrated by, the hypothalamus and parts of the brainstem responsible for sleep, wakefulness and motivation. A small population of cells capable of monitoring changes in ambient light level projects without intervening synapse directly from vertebrate retina to the hypothalamic suprachiasmatic nucleus responsible for circadian rhythms. (For further description see Packard, 2001).

According to this interpretation, the original survival function of the mood change of meteoropaths would have been predictive, both in the statistical and in the

behavioural sense – as, in a Darwinian sense, are all perceptual phenomena (see also Gregory, 1980).

## EVOLUTION OF BEHAVIOUR SPACE AND RELATION TO AFFECT

CEPHALOPODS FROM THE BAY OF NAPLES, SKELETONS FROM THE BERKELEY VERTEBRATE ZOOLOGY MUSEUM

The accelerating pace of morphological change observable in several phylogenetic lines during the Phanerozoic has been ascribed to elaboration of predatory, defensive and other behaviours (see e.g. Vermeij, 1987), reinforced in runaway fashion by behavioural feedbacks acting on such features as relative brain size (brain/body weight ratios) – itself a runaway factor<sup>22</sup>.

To check the hypothesis that behaviour is driving evolution, Wyles, Kunkel & Wilson (1983) employed both anatomical and taxonomic measures to compare rates of appearance of new genera of birds against first known appearance in the fossil record, and found comprehensively that the ten songbird (passerine) ‘orders’ had arisen twice as fast as genera belonging to other orders. This in turn was correlated – by comparing homologous skeletal ratios – with “morphological distance” between specimens of over 200 representative species in the Berkeley zoology museum. Since morphological distance is itself a measure of change in the ways birds use their bodies – *i.e.* “behave” – Wilson was able to link organismal evolution and molecular evolution through the argument that the larger brains and more elaborate behaviours of mammals could change the direction of selection by providing more opportunities (than in smaller brained taxa) for *mutations in regulatory genes* to become fixed<sup>23</sup>.

An attempt to check the hypothesis on a still larger canvas spanning two sub-phyla (!) directly addressed behaviours of Cephalopoda<sup>24</sup> and Vertebrata in the aquatic environment. By ‘behaviours’ was meant abstract organisational features of POL shared by members of the two groups, which as molluscs and chordates are very far apart phylogenetically; comparable measures led to the conclusion that “convergent evolution is evolution of behaviour”<sup>25</sup> and introduced the all embracing term “behaviour space” (Packard, 1972, 1988) as a proper frame for such studies.

Neither of these accounts identified the affective (motivational) sources of behavioural drive, however, nor the critical inherited modifications now known to be epigenetically available at the population level (see main Discussion). Wilson’s ‘cultural drive’ (Wilson, 1985) – illustrated by the early morning habit of opening milk bottles on doorsteps in S.E. England which spread by imitation amongst populations of the blue tit (*Parus (Cyanistes) caeruleus*) – was put in terms of social transmission of information and the potential consequences of learning by imitation, rather than in terms of the birds’ *readiness* to imitate (*i.e.* the ‘felt element’). The search for a satisfactory explanation for the convergent evolution of cephalopods and fish pointed to examples of the actions taking place between predator and prey in shared behaviour space: not to the fundamental motivating forces driving them – for

which, nevertheless, there was first hand evidence from the experiments being carried out in Naples (see above).

## MIGRATORY INSTINCTS AND DEMISE OF THE PASSENGER PIGEON

Migratory instincts are a classic instance of motivational forces at work. Through their relation to reproduction, they put emotional drive at the heart of the evolutionary debate. They can be measured as variations in motor activity; in birds as the restlessness (*Nachtunruhe*<sup>26</sup>: ‘night restlessness’) that precedes their departure on migration. In view of the “observed fast changes and high flexibility of migration” amongst birds (Helm & Gwinner, 2006; Berthold *et al.*, 1992) and interest in microevolutionary effects of climate change, such measurements are once more receiving attention. For some of the great tits (*Parus major*) and pied flycatchers (*Ficedula hypoleuca*) arriving in southern Britain, nesting dates no longer synchronize with maximum food supply (caterpillars) (Dunn, 2004; Robinson *et al.*, 2005) – a “phenological disjunction” that an advance in the timing of hormonal states and associated spring restlessness could in principle correct by precipitating the return flight from North Africa of earlier breeding pairs, to their reproductive advantage<sup>27</sup>.

Enough is known about the habits and numbers of the passenger pigeon (*Ectopistes migratorius*) in the first half of the 19th century to be able to draw a conclusion about its extinction under pressures of hunting and habitat destruction. According to eye witness accounts, the paramount felt need of individuals to stay together in the flock during mass migration left meanders in the flight path of birds established early in the day to be faithfully followed by the millions, perhaps billions, of individuals passing overhead later. Despite numbers once estimated at more than a quarter of the “total bird population of the USA”<sup>28</sup>, the primary urges that drove individuals to this kind of togetherness failed them in the end. We shall see in the Discussion that expression of emotional brain network functions in birds linked to gregariousness and social facilitation can differ quantitatively from one genus or one species to another, and in the lifetime of individuals, subject to simple alterations in the productions of a few highly conserved genes and their receptors (Goodson, Wilson & Schrock, 2012). With or without that kind of phenotypic flexibility – and with or without the handsome reward offered at the end for a single pair (Fig. 8)! – population numbers of *E. migratorius* during its final decades had apparently sunk below levels required to sustain the emotional feedbacks needed for successful communal breeding in this species.

## GENERAL DISCUSSION

*What is the biologist to make of this ragbag of feelings, drives, affection, mood, pain, pleasure, displeasure, appetite, aversion, and conflicting emotions – all labelled as ‘affective component’?* One could argue that it is not the names that count but what they *do*: what is their function? Figure 9 (Appendix 1) places the feedback function of feelings in the comparator of Haukioja’s theory of living entities (POL) monitoring

the state of the organism in its exchanges with the environment over time (Haukioja, 1982). (Since the self-evaluating self-correcting organism [or automaton] central to Haukioja's model<sup>29</sup> is the main agent, not just the subject, of evolutionary change, this places the percepts and intentions encapsulating those feedbacks into the fabric of evolution.)

To turn the question into the kind of practical one facing biologists teaching courses of animal behaviour, what is the student to make of the word 'redundant' in the following much used textbook: "The term 'motivation' has .... its uses in describing how animals 'decide' what to do at any one time. It is the first step in unravelling the complexity of the internal workings of their bodies, a step that becomes redundant as our knowledge of physiology increases." (Manning & Stamp Dawkins, 1998: 193)<sup>30</sup>.

#### EXPLAINING THE ABSENCE OF THE AFFECTIVE COMPONENT FROM FORMAL EVOLUTIONARY THEORY AND WHAT HELP IS AT HAND TO PUT IT BACK

At least for the co-founder of natural selection, the idea that the emotions have been a driving force in evolution was deeply embedded in the theory. It is subsumed in the aggressive or attractive exchanges for instance which take place between individual organisms during competition and sexual selection – two of the main planks of theory – and is inherent in such metaphor as "red in tooth and claw" and "struggle for existence". However, it is *not explicit*. It is neither expressly part of Darwinian theory as nowadays usually understood, nor at the forefront of any attempts to revise neo-Darwinism that we know of. The paradox requires some kind of explanation.

Darwin's interest throughout *Expression of the Emotions in Man and Animals* (Darwin, 1872) is the meaning of the actions of animals. At the same time as writing about their physiological basis – and the last word of the pioneering book is an appeal to the physiologist<sup>31</sup> – he equates them with feelings. "Even insects express anger, terror, jealousy, and love by their stridulation" (Darwin, 1872: 372). The same equation can be found from time to time in *The Origin of Species*<sup>32</sup>. Chapter 8 (*Instinct*) opens with the statement that instincts are amongst the "mental faculties" of animals. And, while explicitly declining any attempt at definition – for "everyone understands what is meant, when it is said that instinct impels the cuckoo to migrate and to lay her eggs in other birds' nests" – it refers to such impulse as a "mental action". With the cultural changes that took place in science and elsewhere over subsequent generations this whole-hearted and uncomplicated acceptance of the affective ("mental") origins of animal action, which was with Charles Darwin from childhood (see endnote 8) is no longer formally acceptable to biologists. An example: Krebs & Davies' (1987) tightly reasoned account of behavioural ecology in terms of costs and benefits and of reproductive success leaves the authors no room to discuss affect as *proximal cause* of instinctual and non-instinctual behaviours; nor realistically can affect be said to be subsumed in the breeding arrangements and changes of hormonal, or other internal state, of the individual organisms discussed in their textbook<sup>33</sup>. Even within emotional sciences "using animal research to understand

pathological fear and anxiety in humans” [Joseph E Le Doux, Wikipedia 2013], Le Doux (2012) argues, on brain circuitry grounds, for non-acceptance<sup>34</sup>.

A further explanation for its absence from formal theory is that there has never been a universally agreed language for talking about emotions. Though there is agreed common language in the biological disciplines (anatomy, physiology, neurochemistry, genetics and molecular biology) that make up the affective sciences (Panksepp, 1998 [2004]), there is still disagreement in the psychological sciences even about what are the basic ‘survival’ emotions (Le Doux, 2012). Cause and consequence, many of the attempts to relate behaviour to evolution, have steered well clear of emotions: a point easily enough checked by consulting the cumulative subject index to the single author contributions in Plotkin (1988). This is also true (see below) of some recent ‘cognitive’ accounts we have consulted. Moreover, none of the 25 contributors to the *Cambridge Companion to the Philosophy of Biology* (Hull & Ruse, 2007) addresses the issues raised in this essay.

When Donald Griffin wrote his book arguing that animals have a mental life and that feelings and emotions are not something to be avoided like the plague (Griffin, 1976: 78), there seemed no way, even for this excellent neuroethologist, to conceive experiments that would break down the conceptual barrier between human and animal. But things have changed. On the one hand, studies of infants (Trevarthen & Reddy, 2007; Trevarthen & Delafield-Butt, 2013a) are building a unified theory of action reliant on these creatures’ deep biological roots, and to which comparative ethologists can easily relate. On the other, a subsequent generation of neuroethologists, armed with immunofluorescence and many other sophisticated techniques exploiting the pattern-recognising properties of molecules, has been able to visualise the location, duration and amounts of activity in parts of the brain known to be associated with emotional responses and to provide insights into their evolutionary role. The “social behaviour network” of teleost fish and passerine birds is found to be homologous to that of mammals, and the genes concerned to be highly conserved; simple variants of these or their expression are able to account for behavioural differences between species, or between individuals living singly and in flocks.

There follows some further information along these lines and discussion of issues already raised.

#### AFFECTIVE EVALUATION: THE INTEGRATION OF PERCEPTION, MOTIVE, AND ACTION

We now need a generation of scholars that are not scared to speak of the raw feelings aspect, and to fully consider the possibility that we are not the only creatures in the world that have such experiences.....but many scientists remain in denial for a variety of reasons (Jaak Panksepp, quoted in Gallagher, 2008)

The gold standard for affects in animals is that learned “reward” and “punishment” effects can be evoked by stimulating brain areas that arouse intense emotional displays, as can be seen in such [hydranencephalic] children, as well as in decorticated animals. The fact that cortex is essentially absent in these cases proves unequivocally that affective consciousness is both generated and felt subcortically (Solms & Panksepp, 2012: 163)

The idea that experience is first and foremost *affective and intentional* (Panksepp, 2005; Delafield-Butt & Gangopadhyay, 2013) meshes with a very ancient lineage of philosophical thought. Alfred North Whitehead (1929) qualifies feeling and its integration as primary sense shaped by the aims of the subject in moment-by-moment events that he calls “actual occasions”.

In mammals, the system evoked by Panksepp & Northoff (2009) as seat of the trans-species “simple ego-type life form” (SELF) generates behavioural repertoires primitively concerned with survival through ‘self-related processing’ of environmental affordance that balances internal need with external affordances (compare Fig. 9); it maps onto brain stem structures tightly integrated with mid- and hind-brain tissues before any mapping onto cortical tissues takes place. Three principal perceptual dimensions are involved: *visceroceptive* sense of physiological status, *proprioceptive* sense of body posture and movement, and *exteroceptive* sense of the external environment (Sherrington, 1906). They suffice for *perception, affective evaluations* and *prospective*<sup>35</sup> engagement with the world already present at birth in humans and other mammals, and the positive/negative bipolar nature of basic feelings as ‘good’ or ‘bad’, pleasant or unpleasant, handled by them carries on through the rest of life. New evidence of motor affective disruption seen in the emotional isolation of human autism spectrum disorder correlates with neuroanatomical disruption in this core brain affective-motor system (Trevvarthen & Delafield-Butt, 2013b). Though anatomically subcortical, the ‘centrencephalic’ core brain system is functionally supracortical. Thus mice or cats which have been surgically decorticated are subsequently still able to navigate tricky terrain, copulate, and wean litters with success (Wood, 1964), and hydrancephalic and anencephalic children born without cerebral cortices but intact midbrains, brain stems and hindbrains are able to develop for many years with planned and skilled use of limbs and hands, engage socially, and share feelings of joy or distress with others (Merker, 2007).

Conversely, if that composition of inter-personal reciprocal gestures and behaviours which creates a social harmony of emotions and movements (Stern, 1985; Trevvarthen, 1998, Malloch & Trevvarthen, 2009), and is part of the development of consciousness and linguistic communication in humans (Delafield-Butt & Trevvarthen, 2013), goes altogether missing following the birth of a human primate, the result can be severe abnormality, psychological and neurological, or simply failure to thrive (Spitz, 1945; Perry, 2002). The human “affect attunement” (Stern *et al.*, 1985), expressed in shared motor acts and autonomic regulation via the vagus nerve (Porges & Furman, 2011), can be saved from global breakdown by fostering, including cross-fostering. On the Amala and Kamala evidence, feelings and intentions towards absent companions in a novel pairing – still reverberating during their first year in the orphanage compound – had been shared successfully enough for the wolf children to survive physically and, by redirecting subsequent development<sup>36</sup>, to thrive.

COGNITIVE VERSUS AFFECTIVE (‘HEAD’ VERSUS ‘HEART’) EXPLANATIONS. CAN BIOLOGISTS CONTINUE TO DISAVOW EMOTIONS IN EVOLUTIONARY THEORY?

Jean Piaget does not explicitly mention drives and emotions in *Le Comportement Moteur de l'Evolution* (Piaget, 1976) [note 'moteur' in the original title: title of English edition simply *Behaviour and Evolution* (Piaget, 1979)], even though they have an important place in the psychologist's life-long work on the child's mental development. As biologist he was influenced by GG Simpson, expressed admiration for Lorenzian and Tinbergian ethology, and critically approved Waddington's ideas on developmental self-regulation. Arguing for what would now be called emergent evolution, Piaget takes the line that "the mechanisms of intelligence itself: anticipations, generalizations, combinatorial systems, compensations, and complementary constructions generating new structures ..... allow the individual subject to discover new problems and to organize with a view to their solution sequences of specific operations" (Piaget, 1979: 89).

The affective component is also absent from the big picture painted by two recent reviews in *Trends in Ecology and Evolution*, though the topic of learning is central in both. The first of these (Verzijden *et al.*, 2012) examines the effects of experience upon mate choice – and thus reproductive outcomes – amongst species of damselflies, butterflies, frogs, fish and birds. They distinguish between the influence of early "preference learning" and "trait learning" upon an individual's later choice of mate, and define both as coming about by "mere" exposure to social stimuli (Verzijden *et al.*, 2012: 511). The authors evoke early imprinting as one of the major mechanisms, but not its drive and motivation content – central issues in the literature on imprinting and critical period etc. (Lorenz, 1966) – still less its affective content. Replacing it with the term "preference learning" begs the question of what feelings or interoceptive value signals (Paul, Harding & Mendl, 2005, speak of their valence) might be involved in the act of preferring.

The second review (Taborsky & Oliveira, 2012) introduces the idea of individual 'behavioural reaction norms' covering the set of exchanges with other individuals; they propose that a flexible phenotypic trait called 'social competence' feeds back upon the epigenetics of brain and molecular mechanisms. Again, this is an input/output cognitive account. Quoting Paul *et al.* (2005), they reason as follows:

... dealing with social complexity requires the evolution of cognitive mechanisms that allow the individual to assess the internal ('emotional') state of other organisms and the social context, and to integrate and process these stimuli not just as a result of direct effects of perceptual information, but rather as a function of what that perceptual information means to the individual at that moment in time . . . Therefore, social decision-making depends on some kind of social experiential knowledge that allows organisms to *evaluate stimuli* [italics ours] and to determine the appropriate behaviour (Taborsky & Oliveira, 2012: 680)

The 'brain social behaviour network' (BSBN) whose neuronal plasticity is manipulated by an individual's 'experiential knowledge' and 'stimulus evaluation' turns out to be made up of essentially the same centres – same network – as are driven by emotions and their neurochemicals (see below)<sup>37</sup>.

We sense an unfilled gap in terminology: between a "neurogenomic state" that is a "transcriptome profile ...for.... expression of a given social phenotype" affecting either neural rewiring or modulating existing circuits (Taborsky & Oliveira, 2012: glossary), and the kinds of dynamic descriptions of brain structure and



functioning during, preceding or following exchanges between individuals that we look for in the language of POL and the credentials of classical physiology (Ludwig & Leng, 2006; Wacker & Ludwig, 2012).

#### PHYSIOLOGY – ENDOCRINES AND NEUROSCIENCE

Classical textbooks of physiology for medical students – a discipline rooted in comparative studies and largely concerned with *regulation* and *control* – devote at least one whole chapter to ‘Physiology of the Emotions’ and their relation to the autonomic nervous system. These texts are unanimous in considering the brainstem and hypothalamic centres for appetites and ‘urges’ of the vertebrate organism as the highest level of control<sup>38</sup>.

In *Homo sapiens*, identification of “the raw feelings aspect” with the chemicals activating them, and synonymy with drugs that have entered the ordinary language, goes back to the early days of comparative neuroendocrinology<sup>39</sup>. As one reviewer has pointed out, the strong case (the “gold standard” of Solms & Panksepp, 2012: 163) for the existence of animal feelings and affective processes in a causal role, consists in the fact that rewarding and punishing human feelings induced by drugs and electrical stimulation typically produce rewarding and punishing effects in animals – even in invertebrates [‘crayfish’ (Huber *et al.*, 2011): n.b. species not indicated]. (For summary, see Panksepp, 2011, and Panksepp & Biven, 2012).

Foremost in the literature must be the 1950s discovery of pleasure centres compulsively awakened by self-stimulation (Olds, 1956). Correlating brain mechanisms across species, though suggestive, are less direct evidence; they lend themselves as readily to cognitive interpretations criticised here as to our non-dualistic interpretation according feelings an organising role.

#### OXYTOCIN/VASOPRESSIN (OT/VP) SYSTEM AND THE MIDLINE SYSTEM

Special focus has been on the neuropeptides oxytocin and vasopressin (Gimpl & Fahrenholz, 2001; Burbach, Young & Russell, 2006; see chapters in Choleris, Pfaff & Kavaliers, 2013) whose crucial role in establishing exchanges with the newborn mammal began this essay.

The pattern of evolutionary continuity with humans in structure and functioning has been found to extend to other tetrapods and fish. Expression of the oxytocin/vasopressin (OT/VP) gene superfamily has been traced in representative species of five vertebrate lineages (Ocampo Daza, Lewicka & Larhammar, 2012) to a time before the separation of cartilaginous and bony fishes. Changes in the sensitivity of their several receptors, which are widely distributed in cortical and subcortical parts of the brain responsible for emotion and memory formation, influence the outcome of social and reproductive behaviours with common links to fear, anxiety, aggressiveness, dominance, approach and withdrawal – even the urge of fish to sing (Bastian, Schniederjan & Nguyenkim, 2001)! Desire to associate with conspecifics is modulated by neuropeptides and/or receptors homologous to those found in humans

(Carter *et al.*, 2008; Heinrichs *et al.*, 2009) and, through dysregulation, the same molecules and/or receptors also affect the mood and social inclinations of certain human personality types (Dai *et al.*, 2012; Montag *et al.*, 2008). Some of the variants of the highly conserved genes involved are single mutations: a source of variation that is quantitatively species- and individual-specific (Gimpl & Fahrenholz, 2001; Goodson & Bass, 2000, 2001; Reaume & Sokolowski, 2011).

That part of the vasopressin/oxytocin system necessary for acceptance of the newborn by the mother goat is located in the projection cells of a primitive olfactory forebrain neural network which transduces odorants directly into mood changes (Insel & Fernald, 2004). A sense of its evolutionary continuity comes from the finding that the network is laid down during development (Belluscio *et al.*, 2002) by remarkably similar steps to those programming the olfactory neuropile of the *Drosophila* embryo (Prieto-Godino, Diegelmann & Bate, 2012). In both, the projection interneurons are guided by the olfactory receptor cells (see also Holland & Holland, 2001): a reminder that the morphological basis of organism/environment reciprocity necessary to successful reproduction in advanced living entities belongs with a “felt element” – smell – as much as does the chemotaxis of primitive ones.

#### IN WHAT SENSE CAN FEELINGS BE SAID TO INFORM THE BIOSPHERE?

The ‘cognitive’ writings we have been criticising sometimes refer to the signal or information content of behaviours without stating what kind of signal is involved and how it is handled by the body. Emotional determinants of action may be perceived differently from what are called ‘cognitive’ ones. The issue is explored by Insel & Fernald (2004) in their review of social information processing. They draw attention to the existence of parallel pathways in the olfactory system of mammals with largely separate genetic controls. The distinction is between a main “generic” sensory system adapted for multimodal processing of complex stimuli (“food, predators, and prey”) and a “dedicated” one consisting of “neurons that project to the accessory olfactory bulb (AOB)” for “species-specific olfactory signals (pheromones) ... that regulate various social behaviors” (Insel & Fernald, 2004: 700).

This raises the question whether *all* sensory modalities have direct pathways for affective information – carrying, say, intermittent bursts of nerve impulses – distinct from the pathways for classic pattern recognition. The question is important to an understanding of the role of behaviour in evolution because of the different heritable factors. On the response side, it has almost become a cliché in the neurosciences to point to the wide ramifications of magnocellular neurones from their brainstem and core brain nuclei into cortical areas with quite different cytoarchitecture (‘wiring diagrams’). The occasional intense firing (Leng & Ludwig, 2006) and hormone-like secretions mediating affective responses of the one are qualitatively quite different (‘analogue’ type) from the pattern-recognizing and memory-forming ‘digital’ activities of the other characterised by specificity of connections, shapes of dendritic fields, and classically modulated impulse frequencies<sup>40</sup>.

It will be seen that we are in complete agreement with the strong position of Panksepp and Northoff. Their claim that amongst mammals “linkage between intrinsic brain systems and the extrinsic world allows brain subcortical-cortical networks to organize a psychologically, emotionally significant and meaningful world within the rest of the brain” (Northoff & Panksepp, 2008: box 1), is one that can be extended *mutatis mutandis* to other vertebrate classes sharing these networks and behaviours: a point made strongly by the Cambridge Declaration on Consciousness (Low, 2012). Clayton & Emery (2007) emphasize the contribution that affiliative behaviours make to construction of the ‘meaningful world’ of corvids (rooks, jackdaws and jays) – some of which rival the reasoning capacities of primates. They are very good at immediate partner recognition, aggression between partners is absent, they spend a long time in expression of mutual affection, such as preening and kissing (compare Fig. 9), and engage in mutual support.

Some experimenters have come close to building a 3-dimensional picture of the changes going on in the “neuromotivational system” of birds that are alone or in flocks, and of fish that sing or do not sing according to changes in sociality or social status. Plots of peptidergic activity and receptor distributions encountered in nodes of the emotional brain network of dominant or submissive, gregarious or territorial individuals have different 3-D ‘signatures’. The idea that they correspond to differences in the amounts of agonistic and affiliative feelings experienced leads James Goodson to the conjecture that evolutionary shifts in bird sociality (group size) “could reflect natural selection on several motivational processes in addition to anxiety and stress, including social arousal, approach-avoidance, reward, and dominance” (Goodson, 2005: 18)<sup>41</sup>.

Our simpler [inverse] view, not unlike that of Allan Wilson (see above), would be that variations in “neuromotivational” state are themselves selecting agents determining the conditions in which natural selection operates.

#### HOW MIGHT INHERITED BEHAVIOURAL MODIFICATIONS FROM SMALL BEGINNINGS COME ABOUT?

The overall impression the non-specialist receives from the technically highly sophisticated studies paraphrased above is that simple variations of ancient genes or their genetic pathways can radically alter expression of the ‘felt element’, and thus potentially alter yes/no outcomes of behavioural exchanges between individuals in a reproductive context. The impression is reinforced if the functions and modifications for which the genes are responsible, going back to the Cambrian, have retained the same *globally integrating* character that emotions have. Changes from gregarious to solitary, non-monogamous to monogamous (Insel & Shapiro, 1992; Winslow *et al.*, 1993), aggressiveness to submissiveness, etc., are exactly the kinds of disarmingly simple switch operating between hypothalamus and ancient cortical brain receptor proteins that could radically shift patterns of breeding behaviour and the conduct of organism/environment relationships in general.

In his famous “tangled bank” vignette which closes *The Origin of Species*, Darwin invites us to reflect on what “laws” have produced the “elaborately

constructed forms, so different from each other, and dependent upon each other” (Darwin, 1900: 669). One major “law” governing that interdependence is adaptive *decision-making through feeling*. Realisation that parts of the brain conducting relations between individuals and evaluating behavioural stimuli have had the same neurochemistry throughout vertebrate history – that despite enormously diversified morphology, the same set of genes and their products are present in the “social decision-making network” and the “mesolimbic reward system” of fish, Amphibia, reptiles, birds, fish and mammals (O’Connell & Hofmann, 2012) – amounts to a demonstration that the same law of emotional decision-making has applied for most of the Phanerozoic.

The theoretical simplicity of the genetic regulation findings in the affective neuroscience field is in strong contrast to the conceptual complexity of the search for correlations between genes and ‘cognitive’ traits – e.g. inherited variants of intelligence, problem solving, spatial learning and other specifically cortical brain functions. That that enterprise has not as far as we know furnished real theoretical insight into the mechanics of evolutionary emergence despite extensive multi-author contributions<sup>42</sup> is one kind of evidence favouring more straightforward hypotheses.

## HYPOTHESIS

Though quite unable to judge the many intricacies of the above, the following seems to offer itself for debate: first, the emotional (affective) component of instinctive behaviour informs the living and non-living world in a qualitatively different way from the learned or ‘cognitive’; secondly, inheritable variants of simple core brain functions that alter the emotional disposition and potential choices of individuals in magnitude or direction are both a principal target of natural selection (*sensu* Mayr, 1997), and a continual source of evolutionary novelty.

## ACKNOWLEDGEMENTS

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## ENDNOTES

- 1 A recent discussion of causation in behavioural biology (Bolhuis & Verhulst, 2009) records the neglect of “‘drives’ in the old ethological sense”, following Tinbergen’s (1963) own criticism of the concept, and the abiding puzzle of how to handle “subjective experiences ... associated with... powerful motivation” (Manning, 2009: xviii–xix).
- 2 In human infants and rat pups the attachment mechanism is first acquired by the foetus on the basis of odour and sound, and can override fear and abusive feedback from the care-giver (see Landers & Sullivan, 2012, for a review).
- 3 See also Corning (2005: 22): “Cooperation as a functional concept ... is found at every level of living systems..... All of the various formal hypotheses about the earliest steps in

- the evolutionary process .... share the common assumption that cooperative interactions among various component parts played a central role.”
- 4 A recent review article on the evolution of human cooperation (West, El Mouden & Gardner, 2011, with >350 references) from one of the oldest departments of zoology, is concerned to bring the theoretical literature into line with neo-Darwinian (Hamiltonian) mathematical modelling, which itself is not challenged. The article chooses a circular logic to define cooperation as “a behaviour that provides a benefit to another individual (recipient), and the evolution of which has been dependent on its beneficial effect for the recipient.” To emphasise this internal logic, the review opens with the astounding statement that “One of the greatest problems for the biological and social sciences is to explain cooperation”. For a summary of some limitations of current neo-Darwinism see Pigliucci (2008: 78, box 2).
- 5 “Prominent investigators are still trying to conceptualize feelings as epiphenomenal species within the higher memorial and linguistic reaches of the brain ... where our highest levels of intentionality are elaborated ... , rather than in the evolutionary ancient emotional processes of the brainstem where the core of mammalian consciousness emerged. I believe those forms of neodualism, that are yielding such wonderful peppercorns of fact, are fundamentally misguided. They do not adequately recognize the natural psychological kinds that arise from intrinsic, evolutionarily provided brain activities, and they continue to be lumbered by a form of dualism that could be resolved straightforwardly if they recognized how mental processes are not only caused by but also realized in certain operations of the brain (Searle, 1983, chapter 10)” (Panksepp, 2000: 250).
- 6 Integration, coordination, adaptation to external conditions through short- and long-term feedback, are built into the science of physiology, and built into the thinking of all major students of evolution. We could call the approach “holistic” if it were not that the word has many different meanings – including being a catch term for none at all (*pace* Bohm, 1980). An approach that always bears the whole in mind, however difficult, is a natural and necessary part of doing good science, whether analytical or synthetic, though “the fact that life presents itself always as organisms remains curiously understated” (Bruce, 2014).
- 7 Poster, presented by A. Packard at the Linnean Society of London meeting, “The Role of Behaviour in Evolution”, 8<sup>th</sup> September 2011.
- 8 We know from his notebooks (accessible at: [darwin-online.org.uk](http://darwin-online.org.uk)) that Darwin, while working on natural selection theory, had already assumed the primacy of the emotions in animal existence long before publication of the *Origin of Species*.
- 9 In market theory, emotions (feelings, affect) are regarded as *vectors* possessing both direction and magnitude that yield useful information on individual and population behaviour. We have not so far encountered such use in the biological sciences.
- 10 For this I (A.P.) have to thank the presence of mind of my home help who arrived at just the right moment. Such knowledge has certainly been around since antiquity.
- 11 The biologist could be criticized for claiming to have empirical evidence of what follows if it were not for the obvious and no less important fact that cross-fostering in the other direction – between humans and canines – is an everyday experience. The case deserves to be much better known. Fortunately the book, published in the US during the early years of World War II, was reprinted in 1966 (see references).
- 12 The account has four pages of notes by Professor R Ruggles Gates (FRS) on the occurrence of this phenomenon in humans (Singh & Zingg, 1942: 19–22).
- 13 Singh, in his diary, draws the conclusion that it was only when the affection of wolf-bonding came to be substituted by that of his wife, that Kamala’s development could be channelled along more human lines – encouraged/reinforced by interest in food. Rather like Darwin, the naturalist in Singh (as much as the priest) makes no distinction *in kind* between human affection and wolf affection.
- 14 In cases of imprinting to a parental figure, its proverbial force is illustrated by the vigour with which his goslings follow Konrad Lorenz and by the striving and distress call of a one-day-old chick separated from its surrogate ‘mother’ (Bateson & Reese, 1969).

- 15 Activation of the prey-capture IRM of young cuttlefish (*Sepia officinalis*) during the days following hatching is similarly delayed by yolk remaining in the digestive system (Wells, 1958).
- 16 The interest here in the method made famous by Pavlov, Skinner, Lashley (and endlessly discussed by them and their followers and critics) is in the universals. Throughout the animal kingdom, above a certain level of nervous organization, reinforcement operates by identical principles that include an obligatory temporal relationship between conditioned stimulus (the 'new' situation) and the unconditioned stimulus: one precedes the other, never *vice versa*, together with feedback associated with the unconditioned stimulus that is value-based (reward/punishment: hedonic/nociceptive). Both match the cause-effect temporal logic of interactions experienced by the subject in the real world.
- 17 One of my first duties (A.P.) at the Stazione Zoologica, Naples was to set up facilities for visiting investigators. These included electrical transformer units supplying different levels of shock (5, 10, 15V AC) for the negative 'unconditioned stimulus' of the trial-and-error (associative learning) experiments, and a daily supply of fresh anchovies for the 'unconditioned' reward. The right quantities of these reinforcers are important for obtaining the subjects' participation and avoid either satiation or aversion to the whole set-up. Level of electric shock is critical. For most *Octopus vulgaris* housed in individual tanks and subject to training sessions involving repeated trials, 15V is too strong a shock, it inhibits all future attacks, while 5V is too weak: insufficient to deter attacks on the 'negative' by an inquisitive animal weighing some half kilogram and well adapted to captivity.
- 18 To forestall potential criticism for equating experimental 'reinforcement' of response in the laboratory with the affective component, or role of 'affect' in natural behaviours generally, it may help to point out that in the case of octopuses we are not dealing with Skinner boxes and scores achieved in automated experiments. The Naples *Octopus* experiments have been criticized by the North American school of comparative psychology for what amounts to the experimenter's involvement with the animal subject (see Boal, 1996) but, in terms of the insights afforded, an inter-subjective approach has been part of their strength.
- 19 In the original photograph (Packard, 1963: 41, plate) for Figure 7, from Packard & Sanders (1969: 94), the animal wears the 'conflict mottle': a colour pattern that combines the dark of approach and pale of withdrawal, more deeply contrasted on the side of the body directed towards the ambivalent target than away from it (see Fig. 7 inset).
- 20 See also multi-author proceedings of meeting on ritualisation organised by Julian Huxley (1966b).
- 21 The word meteopathy is absent from most English dictionaries, but is quite well known in other languages, such as Italian.
- 22 The relative brain size-curve for major vertebrate groups plotted against estimated time of origin on a 400 million-year scale is *more than exponential* (!) (Wilson, 1985). An example of the reverse trend from the fossil record of island Bovidae, when predation pressure was removed, is given by Köhler & Moyà-Solà (2004).
- 23 "Pressure to evolve comes from the brain of mammals and birds. This internal pressure, a consequence of the power of the brain to innovate and imitate, leads to culturally driven evolution. Once a species has a dual capacity to evolve, a new way of exploiting the environment can arise in a single individual and spread rapidly to other individuals by imitative learning. By suddenly exploiting the environment in a new way, a big-brained species quickly subjects itself to new selection pressures that foster the fixation of mutations complementary to the new habit" (Wilson, 1985: 172).
- 24 Mangold-Wirz & Fioroni (1970) ranked the cephalopods [class Cephalopoda] as a sub-phylum of phylum Mollusca.
- 25 The claim was not limited to that one spectacular history over the last 400 hundred million years. "It carries the lesson that even such important features of an animal's organization as the mode of locomotion, the structure of the feeding organs, the transducing capacity of the sense organs and degree of development of the brain do not

themselves determine the course of evolution; rather they are presupposed by and come to be modified by, the *system of behaviour* [italics added] within which they operate. In those areas of the system where cephalopods and vertebrates directly interact, the outcome of the competition centred upon food has been a broad adaptive zone shared by animals of radically different origin and organizational type. It is as if natural selection had favoured those that took the line, 'if you cannot beat them, join them'." (Packard, 1972: 296.)

26 Names have changed: "*Zugunruhe*" (migratory restlessness) avoids the implication that restlessness is necessarily nocturnal but the finding that non-migratory species show the same seasonal restlessness as closely related species about to travel (Helm & Gwinner, 2006) suggests that another term is overdue.

27 For such a shift to occur, it is not necessary to invoke a change in cognitively perceived environmental cues at the place of departure.

28 [http://www.si.edu/Encyclopedia\\_SI/nmnh/passpig.htm](http://www.si.edu/Encyclopedia_SI/nmnh/passpig.htm);  
[http://en.wikipedia.org/wiki/Passenger\\_Pigeon](http://en.wikipedia.org/wiki/Passenger_Pigeon);  
[http://www.stanford.edu/group/stanfordbirds/text/essays/Passenger\\_Pigeon.html](http://www.stanford.edu/group/stanfordbirds/text/essays/Passenger_Pigeon.html)

29 See also Bruce (2014), this volume.

30 The quotation seems to suggest that the abiding Tinbergian (Tinberg, 1951) dilemma of the subjective experiences of animals not being open to empirical analysis can be dissolved by attrition. On the grounds that "*the only scientific view of consciousness is that we don't understand how it arises*" (Stamp-Dawkins, 2012b), Marian Stamp-Dawkins now uses the agnosticism to educate in favour of the humane treatment of animals (Stamp-Dawkins, 2012a).

31 "We may well conclude that the philosophy of our subject ... deserves still further attention, especially from any able physiologist" (Darwin, 1872: 390).

32 For instance "*desire*" and "*restlessness*" are amongst the words used when discussing how a 3-days-old cuckoo's instinct to eject the foster parents' young from the nest may have originated (Darwin, 1900: 333–34).

33 Even in the relation of feeding to hunger: "the traditional view that an animal's internal state controls its behaviour can be turned on its head and the animal can be seen as using its behavioural repertoire to control the internal state in an optimal way" (Krebs & Davies, 1987: 65–66).

34 The recommendation that "we should resist the inclination to apply our introspections to other species" (Le Doux, 2012: 666) hardly strengthens the argument against ascribing feelings, since the author omits distinction between introspection and intuition – which plays an important role in science.

35 The term *prospective* reflects the simple biological truth that all adaptations have both a present and a future reference; the central nervous programmes for action (Young, 1978) are by definition prospective [as 'programmes']. See also Gregory (1980).

36 In view of the comparative sweep of this essay, it is important to note that the behavioural and *developmental plasticity* woven into the biological fabric of the wolf children is greater than anything observed following everyday cross-fostering experiments in the inverse (canine to human) direction.

37 "Two major mechanisms of neural plasticity operate at different time scales: structural rewiring of neural circuits is slow and long-lasting and induces dramatic behavioural changes, whereas biochemical modulation of existing neural networks is postulated to mediate fast and transient changes between motivational states that promote gradual changes in behavioural expression" (Taborsky & Oliveira, 2012: 679).

38 Many have pointed out that the future hypothalamus and subcortical–cortical midline structures (SCMSs), with their wide ramifications into other parts of the brain, occupy the same location at the front end of the neural tube, and close to the midline, as the embryonic organiser: originally the dorsal lip of the blastopore. See Holland & Holland (2001) for further enlightenment and origins of the olfactory placode.

39 In his lectures to the Harvard medical school describing results of electrical stimulation of the diencephalon in the intact cat, Nobel laureate WR Hess argued for speaking of the

- “anger” of a cat rather than “sham rage”: its equivalent being investigated in the decorticated animal by Sherrington and colleagues (Hess, 1954: 17–21). Since there appeared to be no difference between them, Hess is saying that “anger”, both expression and experience, belongs with ancient core brain not with missing neocortical brain.
- 40 For an account of the involvement of *affect* in the well-known cortical brain processes of visual pattern recognition in mammals and its relation to low spatial frequency (‘primal sketch’) aspects of the input, see Barrett & Bar (2009).
- 41 Proximate mechanisms related to stress, dominance, appetitive approach/avoidance and reward could hypothetically interact in multiple ways to yield species variation in social structure (Goodson *et al.*, 2005).
- 42 See Coghlan (2007).

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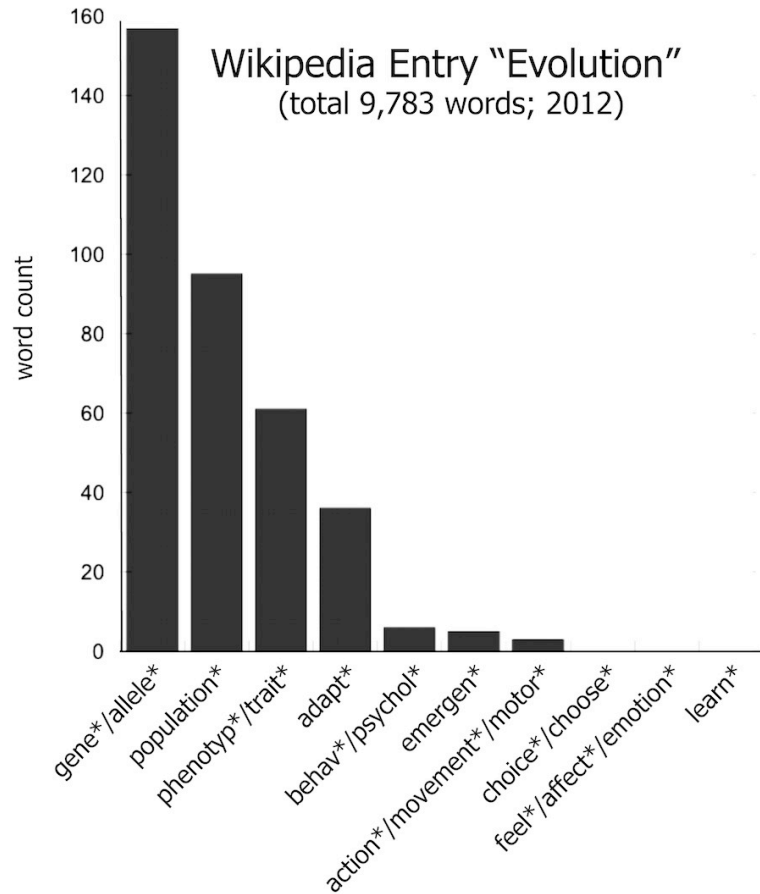
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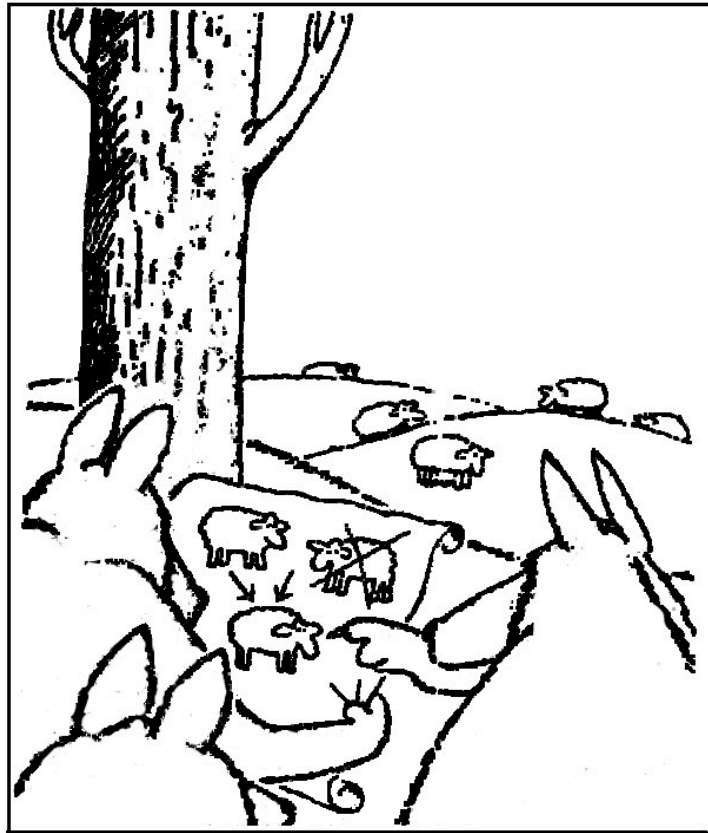
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## FIGURES



**Figure 1.** Current consensus on 'Evolution in Biology' amongst the Wikipedia community indicated by word frequencies used for the English language featured article <http://en.wikipedia.org/wiki/Evolution>. Counts for "gene/allele", "population", "phenotype/trait", "behaviour/psychology" and "emergent" include occurrences in references (but not links). Hits for common words other than those plotted: one hit for "act", no hits for "drive", "motivation", "modify" "choice", "choose", "learn", "learning", "memory" "reinforce[ment]" "affect", "feeling", "emotion". Editorial history statistics (February 2012): *ca* 14000 total revisions since 2001 undertaken by *ca* 4000 users. Number of edits made by the top 10% of active users: 8,518 (62.27%).

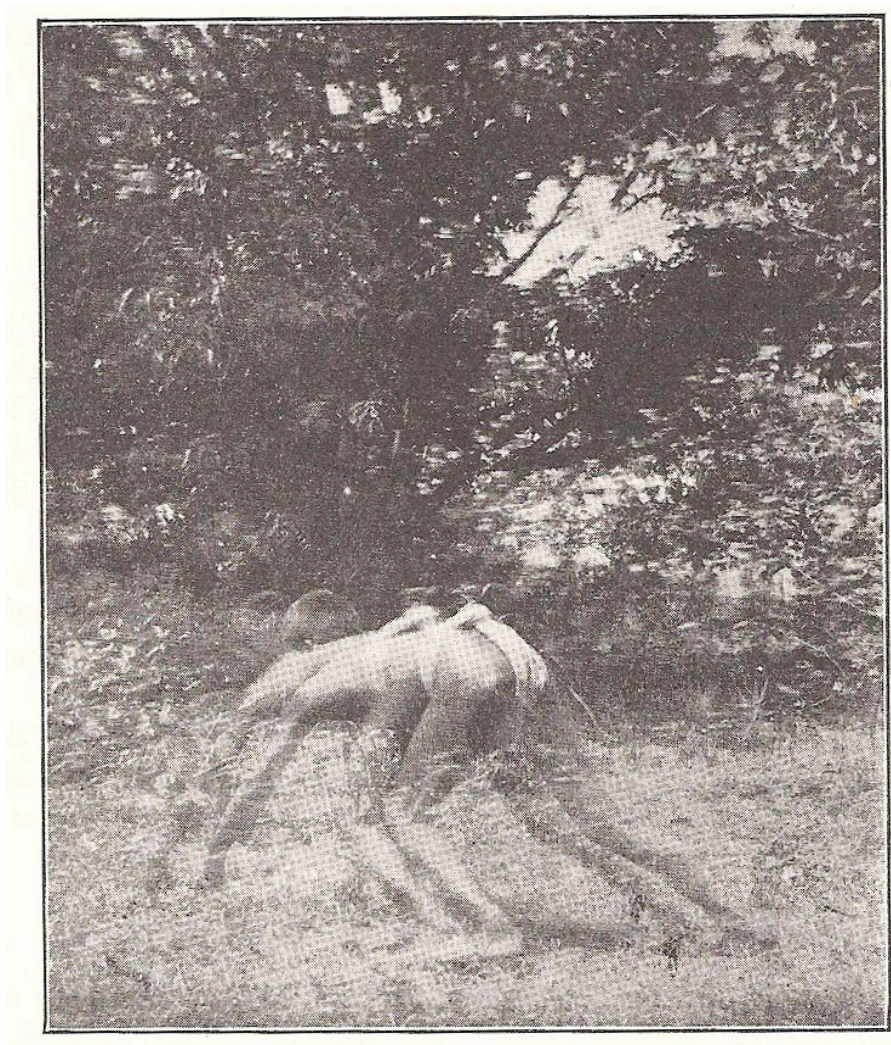




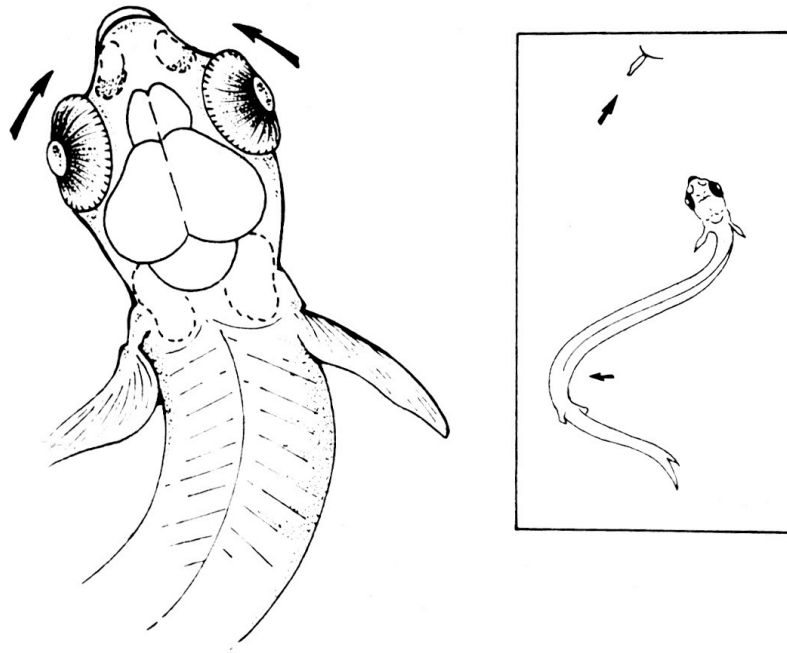
**Figure 2.** "Natural selection at work". (Cartoon by Gary Larson: redrawn.)



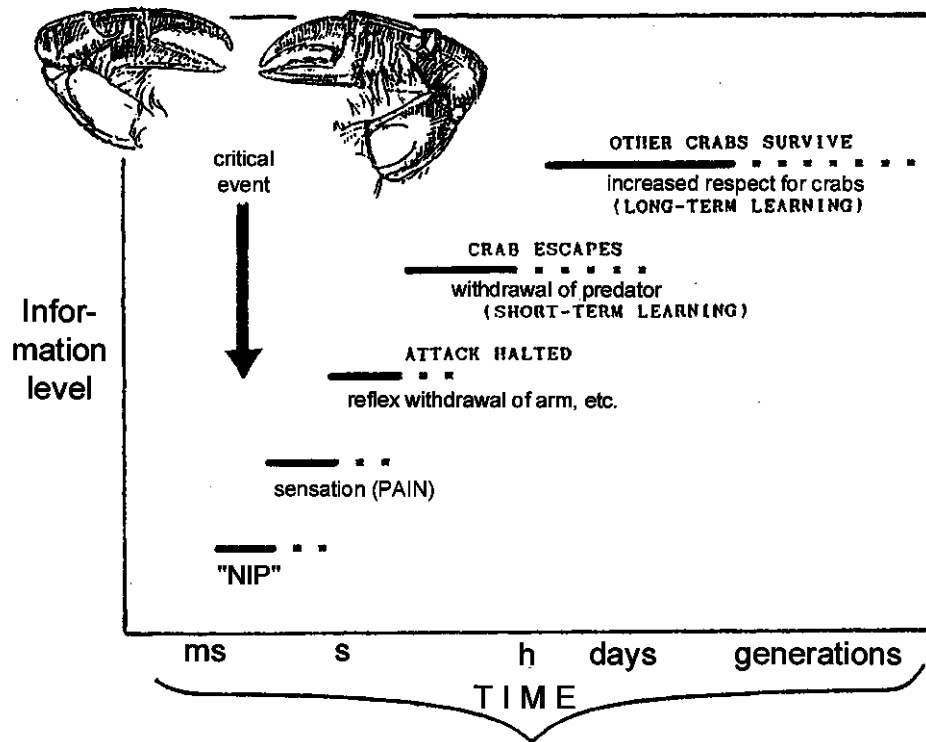
**Figure 3.** Mythical scene depicting behaviours associated with suckling. (Detail of the fresco *Hercules and infant Telephus*, unknown artist, Naples, Museo Nazionale, ca 50 AD.)



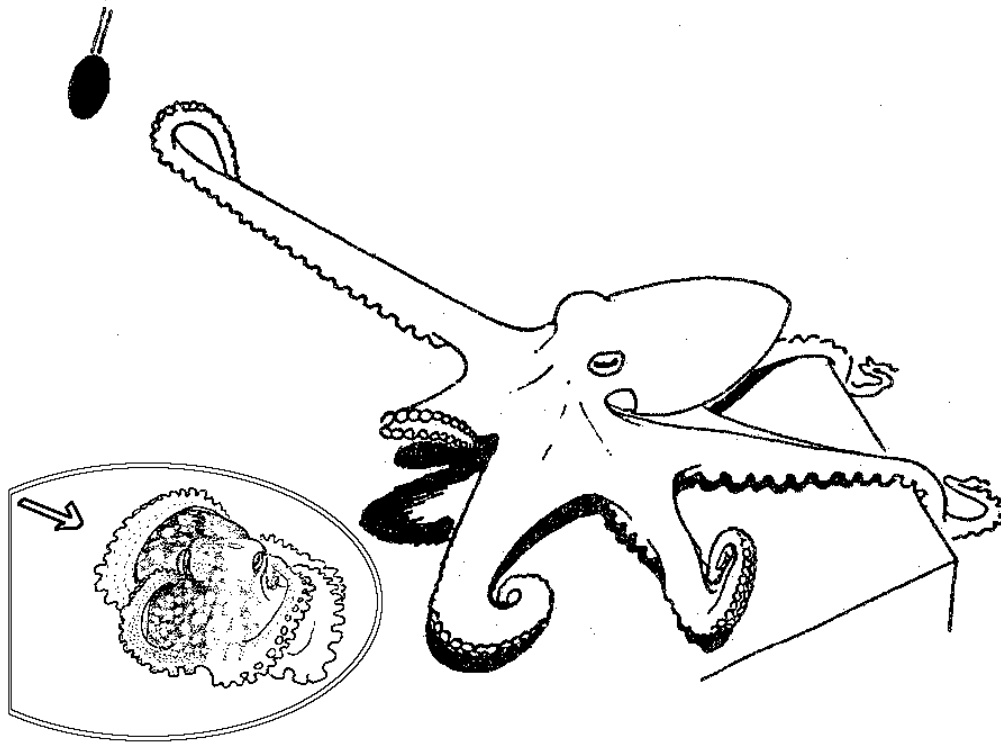
**Figure 4.** Double-exposed Kodak snapshot of the wolf-child Kamala by J.A.L.Singh *ca* 1921: “mode when running very fast”. (Singh & Zingg, 1942: 30.)



**Figure 5.** “Visual grasp reflex” of a “pause-travel” predator (*Clupea harengus*). Upon depletion of its endogenous food supply (yolk) the larval herring is preparing to strike at a potential prey (copepod). Inhibition of forward swimming, S-shaped flexion of the body and vergent eye movements are mediated by large midbrain tecta seen through a transparent braincase (ventral midline diencephalic structures responsible for ‘appetite’ not seen). Right image from Rosenthal & Hempel (1969), left original.



**Figure 6.** Octopus vs crab: one-trial learning. Time course, and potential evolutionary consequences of an encounter between a hungry juvenile *Octopus vulgaris* attempting to prey on a crab (*Carcinus mediterraneus*) of much the same size as itself. The prey has repulsed the predator with a “nip” from its claws (seen upper left from the side of the crab). (Modified from Packard, 1990, based on a video recording made in one of the glass aquaria of the laboratory, Naples Zoological Station.)

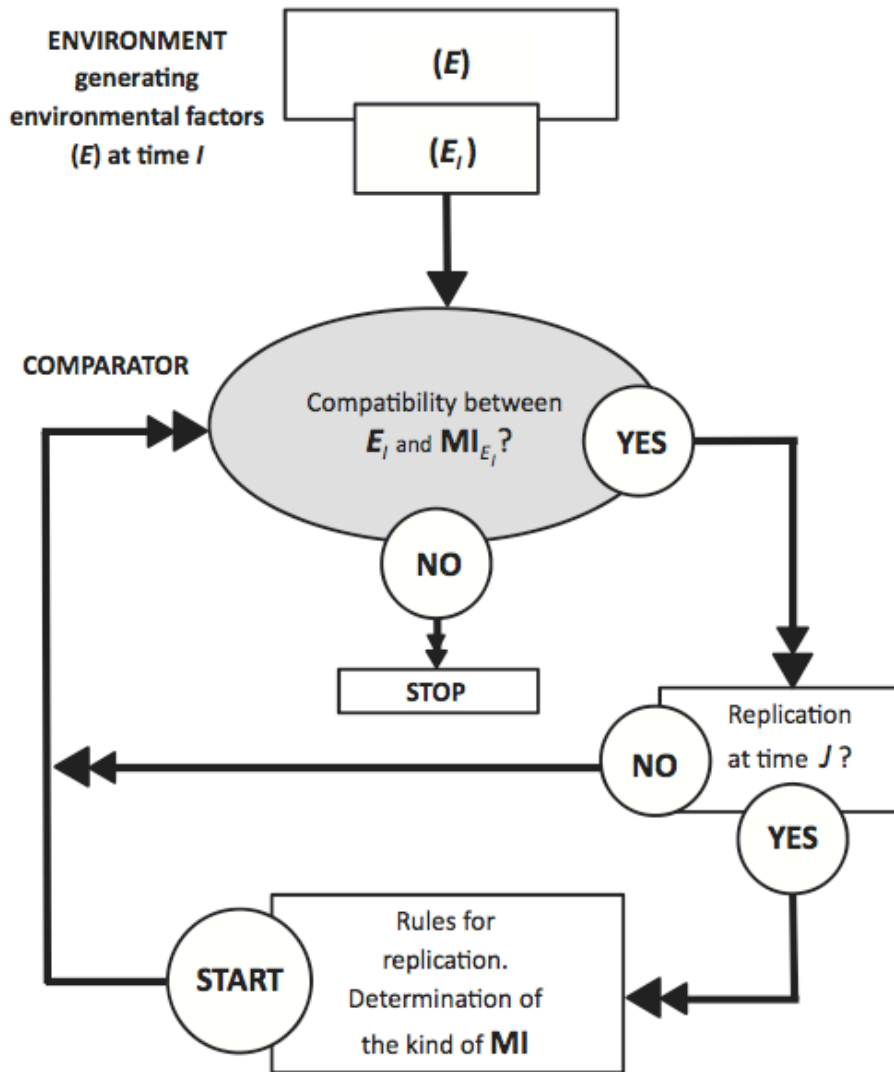


**Figure 7.** Postural conflict in octopus. A combination of approach and withdrawal components during cautious approach to a negative stimulus (see text). Inset: the ambivalence is seen in the “conflict mottle” colouring of an animal expressed towards an intrusion (arrow) coming from one side, see text. (From Packard & Sanders, 1971.)





**Figure 8.** John James Audubon's 1824 portrayal of *Ectopistes*. (From engraving in Mershon, 1907, *The passenger pigeon*, now in public domain.)



**Figure 9.** *Process of Living* flow diagram (from Haukioja 1982: 363, fig. 2; graphics modified) summarises Erkki Haukioja's *Theory of Living Entities*. Double-headed arrows are one or more *self-evaluating individuals* (automata) *persisting in time*. The evaluation process ('?') taking place in the comparator corrects for discrepancies between environmental factors ( $E$ ) at a given moment ( $E_I$ ) and maintenance information (MI) relevant to those factors at that moment ( $MI_{E_I}$ ). Haukioja distinguishes between maintenance information (MI) and reproductive information (RI), both of which make up operative information (OI): i.e. the instructions produced when the genetic or other code is translated. In POL, the criterion for success of organisms is persistence over time as measured by their ability to maintain themselves at the moment of evaluation (Haukioja, 1982: 360), rather than measured at some future time. In our scheme (see main essay), the *question mark(s)* ('?') in Haukioja's comparator box monitoring the state of the organism in its exchanges with the environment would symbolise the 'felt-element' (emotion, or affective component).